

## SIR WILLIAM MACLEAY MEMORIAL LECTURE 1970

### VARIATION — THE ESSENCE OF LIFE

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[Delivered 29th July 1970]

Sir William Macleay had the great distinction of being able to identify vital needs of natural science at a time when in Australia few men of science, let alone men of affairs, thought about broad issues involving science. His great collections set a pattern which we are attempting to follow in the Biological Survey of Australia—still only a proposal by the Academy of Science to the government. His imaginative and generous support for post-graduate research was well ahead of the times, as was his recognition that science needed both substantial financial support and sound organization. And, as the lecturer of 1962, Professor R. N. Robertson, emphasized, Sir William had remarkable prescience in discerning important fields and issues. These qualities have given me encouragement in preparing this lecture devoted to Sir William's memory.

The lecture examines the conditions for the long-term conservation of life and of the habitats necessary for its survival. I shall maintain that genetic variation is an essential condition for continuing evolution, hence for the continued existence of domesticated as of wild biota, and on this basis I shall attempt to outline biological principles for long-term conservation. The endeavours of the pioneers of conservation in Australia to salvage valuable communities and areas have created the conditions in which a national plan based on biological principles has a chance of wide support.

#### ORGANIC AND CULTURAL VARIATION

Variation—the essence of life: what a trite phrase, how very obvious! Clearly, genetic variation is universal, ubiquitous, in space and in time. Life could not have evolved without it, and any restriction of variation tends to restrict the evolutionary potential. Natural ecosystems depend on variation for their adaptability and long-term stability; by contrast, man-made agricultural systems are near-invariant and depend on man for sustenance, protection and genetic adaptation. Divorced from nature in our urban living, we seek for recreation the scenic variation, the multiplicity of life forms in a natural landscape. But now, throughout the biosphere, we are faced with a mounting *loss of variation*. This threatens the quality of human life, and the continuing existence of other living beings. I shall argue that *variation needs defending* if life as we know it is to survive.

Variation is so strongly built into our own lives that we take its pervading existence for granted. We vary from day to day, from year to year, from birth to death. We vary our food, as did our ancestors at the beginning of civilization 10,000 years ago. Our attitudes, tastes and styles vary in time, with major and minor cycles. Periodically, sometimes between generations, we experience a drastic change, triggered, it would seem, by a kind of socio-aesthetic Oedipus complex, a dislike for the attitudes and tastes of our fathers. As an evolutionist one may be tempted to interpret this,

like its prototype in individual psychology, as an adaptive device to generate behavioural variation as the raw material for cultural evolution. Short-term cultural cycles, or fashions, are almost as ancient as civilization; lately they have become shorter and more drastic, doubtless in response to technical capabilities and artificially created, often resource wasting, economic impulses. But I have a sneaking feeling that the growing uniformity in the world around us helps to generate a desire for symbols of an ephemeral cultural variation, in spurious compensation for the erosion of biological and ecological variation which is occurring under the impact of the technological revolution.

I am leaving these analogies between organic and cultural variation with some reluctance, since I believe that our attitudes and behaviour patterns are highly relevant for the future dynamics of variation in the world at large. For now that man has become the master and controller of variation, as of everything else, *our* attitudes, *our* insight, *our* interests—variable and often contradictory as they are—set the pattern of variation for landscape, plant and animal life, and no doubt before long for our own species. Clearly, for an understanding of processes which to an increasing extent are directly or indirectly controlled by human activities, one must turn as much to the social and behavioural sciences as to the biological and physical sciences and to their recent integration, environmental science. Finally and most importantly, if a sense of responsibility towards the present and the future state of the world is to become a potent force in human affairs as it must if life on earth is to survive, social ethics and what might be called evolutionary ethics must become effective and influential partners in decision making.

#### VARIATION IN CULTIVATED PLANTS

Man's control is closest over species or communities which are as dependent on man as man is on them—the domesticated plants and animals. Having evolved, to use Vavilov's phrase, "at the will of man", they are dependent on man for the provision, development and conservation of the genetic diversity which is an essential condition of continuing evolution.

None of our domesticated plants or animals are older than civilization itself—a mere 10,000 years; and although the historical evidence is scant and evolutionary pathways have been complicated by man's interference, the record has been filled in by taxonomic, genetic, ecological and archaeological research. In consequence we have now a considerable body of information about the antecedents of our cultivated plants; and although we know in no case the place or mode of origin of a domesticated plant (or animal), we have a broad picture of the patterns of variation which now exist, and of their historical background. Hence we know a good deal more about variation in many domesticated plants and animals than in all but a handful of wild ones.

The generalization is valid that through the period from the beginnings of domestication to the present, but especially in recent times, there has been a progressive reduction of species diversity which is still continuing. The most common pattern which is apparent today derives from the transition of a generalized natural ecosystem to a specialized artificial ecosystem, involving a drastic reduction in diversity (D. R. Harris, 1969).

During the transition period from hunting-fishing-food gathering to domestication of plants and animals, a great variety of plant and animal species were used, with the distinction between "gathering" and "cultivation" gradually emerging. At Tepe Ali Kosh, in south-west Iran, Helbaek found in excavations dating from the early beginnings of domestication (7500–5600 B.C.) seeds of forty-odd plant species and bones of about thirty-five animal species;

two of the former and two of the latter belonged to domesticated species. The total number of species greatly exceeds that used today in the same region. During the following millennium the inhabitants of Tepe Sabz, also in south-west Iran, used at least seven domesticated plant species (including nine distinct types) and three domesticated animal species. As the number of domesticated species increased, the number of wild species used for food decreased (Flannery, 1969).

With the spread of agriculture in Afro-Asia and in Meso-America, plants, animals and man, as Darlington (1969) observes, evolved in close interaction. Selection produced crops from wild plants or from weeds, which, as colonizers of disturbed environments, were already pre-adapted for cultivation (Hawkes, 1969). Others, like our hexaploid wheats, originated from the combination of wild and domesticated species. The number of cultivated species increased with the rise of civilization and the differentiation of human needs, and with the spreading of settled agriculture into regions which made their own contributions, such as the numerous tropical fruit and vegetable species originating in south-east Asia and Meso- and South America. Quoting Mangelsdorf (1966), "during his history, man has used at least three thousand species of plants for food and has cultivated at least one hundred and fifty of these to the extent that they have entered into the world's commerce." But, Mangelsdorf continues, there has been a tendency to reduce the number of crops to those which are the most efficient; and "today the world's people are actually fed by about fifteen species of plants." It should be noted, however, that this process applies in the main to staple food crops. A number of wild species have been taken into cultivation even in the last hundred years—as pasture plants or for soil conservation, as industrial or medical plants, or as ornamentals; and, as Brücher (1968) points out, there is as yet a reservoir of potentially useful indigenous plants in South America, and, one may presume, in other tropical regions.

As the number of major food plants declined, variation *within* species increased. This has been the case especially with the ancient staple food crops which spread early in their history from the region in which they originated into others where they acquired further diversity. In this way the gene pools of our major crop plants were greatly enriched. When wheat reached China three thousand years after its domestication in the Near East (Darlington, 1969) many types evolved which are peculiar to that region. Some, very likely evolved under irrigation, have ears with unusually large numbers of spikelets and spikelets with unusually large numbers of grains. Wheat, like so many other good things, was carried across the sea of Japan and one may guess that it was this character combination which centuries later reappeared in a modern Japanese wheat, Norin 10, to find its way into Vogel's record yielding hybrids (Vogel, Allan and Peterson, 1963) and ultimately into Borlaug's Mexican varieties (1958) which are saving India, Pakistan and other developing countries from imminent starvation.

Altogether Vavilov (1951) described nine centres of genetic diversity. Some of these were places of origin for some crop plants, of diversification (secondary centres) for others. The formation of secondary centres, however, did not end in ancient times. Valuable gene centres derived from post-Columban introductions of American plants to Asia, the Pacific region, Europe and Africa, and of Asian crops to America. Nor did evolution stand still within the ancient centres themselves. Local landraces remained in balance with the environment, subject to the gradual changes which occur under conditions of subsistence agriculture. Some areas still retained the evolutionary opportunities of introgression from related weeds, and from wild species on the edges of the fields (Harlan, 1951, and Bennett, personal communication on wheat in Afghanistan). But even where this was not the

case—as in many secondary centres—local varieties retained their enormous diversity and their distinctive character, often differing from valley to valley, from hill to plain; and, in the absence of deliberate selection, the populations retained the adaptive variability which was essential for their—and their cultivators'—survival in a primitive agro-ecosystem. This was still the position at the time Vavilov made his discoveries in the 'twenties and 'thirties.

Diverse as they are, the gene centres have one feature in common—they are located in what we now call the developing countries. In the *developed countries* of the Old World, the ancient landraces had begun to give way to plant breeders' selections in the middle of the last century, resulting in a steadily decreasing number of "pure" varieties of superior agricultural merit. Inter-varietal diversity had been greatly reduced and intra-population variation lost altogether. Introductions from various parts of the world began to enlarge effective gene pools, especially in the newly developing countries of North America and Australia where indigenous genetic resources were non-existent. But everywhere there was a tendency to restrict rather than enlarge the parental circle (Frankel, 1954).

Not until Vavilov's discoveries was there a realization of the extent of the variation which was to be found in the as yet undisturbed centres of genetic diversity. Plant exploration became widespread in the decade before the last war, but not even in potatoes—probably the most intensively surveyed genus—was it exhaustive. None equalled in scope the collections of the Vavilov group, and none, including the Russians, had the vision that collections maintained alive were bound to erode, and that the gene centres themselves might not last forever. To sum up, the varieties in use today for the most part have a narrow genetic base, with only a fraction of the existing variability used by, or available to plant breeders. To the present day the genetic resources embodied in the primitive agricultural flora have not been adequately surveyed, let alone collected or maintained.

In the *developing countries* it was not until the 'thirties that selections from indigenous material and introductions from elsewhere slowly began to spread in the backward regions which harboured, and in their backwardness guarded, the genetic treasures; but the avalanche came in the last two decades. Now the spread of modern technology is sweeping away outlived forms of production, and with them the ancient genetic heritage. Agro-ecosystems with intensive cultivation, fertilizer application, plant protection, weed control, and, where possible, irrigation, require varieties adapted to high productivity levels rather than to the rigours of primitive husbandry. Such varieties are the new Mexican wheats and Philippine rices, high-yielding strains of hybrid corn and hybrid sorghum, and soon many more. Some of them possess broad adaptability, but where needed they can be tailored to local conditions. Over wide areas in Asia, Africa and Latin America, where genetic diversity was widespread and seemingly inexhaustible in Vavilov's time, it has all but vanished, and it will have done so almost everywhere within a decade or two; and this includes all the major and some of the minor plants used in agriculture and horticulture, and even some gene pools of importance to forest tree breeders. The green revolution is saving hundreds of millions from the threat of hunger or want, but at the price of losing the genetic resources which are indispensable for future plant breeding and for all types of research on cultivated plants. Here I must refrain from discussing the significance of this material for plant breeding and other kinds of research, and refer to a just-published book by a representative group of authors.\* However, a brief discussion of the *conservation of variation* in

\* Genetic Resources in Plants—Their Exploration and Conservation. (Eds. Frankel, O. H., and Bennett, E.) Blackwell, Oxford, 1970.

domesticated plants is appropriate since it is part of the general problem of the conservation of variation.

To conserve modern varieties presents no special problems since they are part of the current agricultural system. But the primitive landraces evolved and survived in primitive agro-ecosystems which are rapidly becoming obsolete in the regions where the "genetic treasuries" still persist. Conservation *in situ* requires the retention of the ecosystem as a whole, including the cultivator. On the scale needed to preserve gene pools spread over wide areas this is impracticable on social, economic and technical grounds. As a rule it is therefore inevitable to remove the material from the areas in which it was cultivated to places of safe-keeping in scientific institutions. Inevitably this incurs the risk of genetic change through natural hybridization, selection or genetic drift, and methods of conservation must seek to minimize these risks.

The only practicable method of conservation is to "freeze" variation in a steady state, to be "unfrozen" for use in plant breeding or research when required. For seed-reproduced plants, and especially for annuals or short-lived perennials, long-term seed storage is the only safe and practicable way. Storage technology and seed physiology have reached the stage when safe storage over long periods can be obtained for many species. Regeneration must take place under conditions minimizing natural selection. Asexually reproduced plants, and especially long-lived trees, can be, and often are, preserved in living collections, plantations or orchards. Being mostly highly heterozygous a small number of individuals represents a range of genetic variability.\*

There is now a wide-spread awareness of the imminent threat to the existence of the centres of genetic diversity. World-wide interest has been aroused in the collection and conservation of material before it is too late. The Food and Agriculture Organization of the United Nations (FAO), the International Biological Programme (IBP), foundations and national organizations are engaged in a survey of material in existing collections and in the centres of diversity themselves. The urgency and importance of this rescue operation is now widely recognized, and hopes are justified that this will lead to the first world-wide effort in the conservation of genetic variation.

#### NATURAL COMMUNITIES

And now we must turn to the natural communities which, though exposed to human influence, on the whole depend on their own devices for their continuing existence. Some, such as natural forest and range communities, or fresh water and marine fisheries, are subject to exploitation and a measure of control. Others are left in a natural, or near-natural state, either because they are deemed unsuitable for exploitation, or as reserves for a variety of purposes—forestry, watershed conservation, recreation, nature conservation, scientific studies, wilderness areas, or others.

Natural communities are ecosystems in balance with the environment. Even the simplest are systems with a complexity of components and interactions which as yet we are unable completely to unravel. A major step towards a fuller understanding will come from the multi-disciplinary, integrated studies of major ecosystems which form part of the International Biological Programme. But it has long been recognized that a crucial, indeed wholly basic feature of natural communities, a feature which distinguishes them from all man-made systems, is their infinite diversity, as basic for their *functioning* as it is for their survival and *continuing evolution*. It is also,

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\* For a fuller discussion of the conservation of cultivated plants I refer to Frankel and Bennett (Eds.), 1970, chapters 40-44, and to Frankel, 1970.

I believe, the main reason for our own often passionate involvement in the continued existence of wild communities and of wilderness areas.

Let us first consider what natural communities give to man, before considering what we can do for them. To modern man, living in urban surroundings as most of us do, "unspoilt nature" as we so meaningfully refer to it, is a cause of aesthetic delight, emotional attachment, and, to a growing extent, of profound and absorbing scientific interest. One need not go as far as Nigel Calder's utopia of the society of the future which will find its release from almost workless boredom in an "environment game" of ecological observation, research and management. But even now there is a widespread and increasing interest in studies of natural communities in their infinite adaptive variety. There is a growing recognition that they are not only essential factors in the long-term stability of climate, the purity of water and air, the maintenance of carbon dioxide levels in the atmosphere, but that they provide a focus for the wise and conservative use and management of natural resources, a link between the sciences, the nations—and even between the generations. A powerful reason for this rapidly growing interest in wilderness and wildlife is the widespread realization that all too little is left, and that what remains is in danger of erosion or extinction. Population growth, industrialization and urbanization put increasing pressures on the remaining natural areas, through encroachment and the general deterioration of the environment. It is becoming increasingly clear that in times to come only areas which are dedicated and secured as nature reserves by law or by covenant, are likely to retain a major degree of natural integrity. This realization is responsible for the rapidly growing demand for more adequate nature reserves, especially in the most highly developed areas of the world. Already population pressure has become a major problem for national parks in the United States, demonstrating not only the growth of public appreciation, but the urgent need for a forward looking policy on nature conservation.

In Australia we still have great, though not any more limitless opportunities for nature reserves on a grand scale, with an agreeable, or at least tolerable climate throughout the year, a wildlife of tremendous variety and interest for scientist and layman, a diversity of form and colour in a landscape of peculiar and often subtle beauty. Besides, and perhaps above all this, large areas of the country still have an asset which is truly unique and will be increasingly valued by urbanites all the world over—spaciousness and solitude. Where else can one walk, or even drive for days without seeing another human being? And even the development of tourist facilities, if planned so as to give some weight to other than purely commercial considerations, should not seriously interfere with the pursuit of solitude in an environment where the mass-produced human can recover a sense of his individuality as a unique variant of *homo sapiens*.

For this to be achieved we need *large reserves*, kept intact as near as possible in their natural state. Where on earth are there better opportunities? Indeed, where on earth are there still opportunities of areas so vast, and so low in economic productivity that even a modest share of what can be foreseen as the tourist industry of the world in the twenty-first century, will beggar the present and foreseeable pastoral output in our arid areas? If we had now the kind of United Nations of which one may dream among things to come, it would enjoin upon Australia to declare large parts of its central regions a grand reservation where land use would be largely subjected to nature conservation. By the time the United Nations gets round to it it will be too late. So it is up to the Australian government and people to have and use the imagination, foresight and wisdom which alone can safeguard an incomparable and irreplaceable resource for Australia and the world.

But even the largest nature reserve—and one on the scale I have suggested would be truly tremendous—cannot satisfy the needs or the responsibilities for nature conservation of a continent extending from the tropics to the cool temperate zone, with a corresponding range of indigenous vegetation and animal life. Australia takes a prominent part in an important IBP project which has undertaken to identify and classify the distinct plant communities throughout the world, and to ascertain the degree of protection which is afforded to each of them. In Australia the work is nearly completed and some seven hundred communities have been identified. It is conducted by expert committees in all states and coordinated by a national committee under the chairmanship of Professor R. L. Specht, of the University of Queensland, who, in his earlier work in South Australia had set the pattern for these surveys. This world-ranging survey will chart the realities of communities and the extent to which they are protected. It will serve as a guide for local authorities, governments, international organizations, and for scientists and citizens concerned with the conservation of nature.

How far such blue prints will serve as a basis for *action* will depend on economic, social and political pressures and on the direction and strength of public consciousness. However, these problems are not the subject of this lecture. I am concerned with the biological parameters which determine whether a population has the potential to persist, adapt and evolve, within the context of the physical and biological environment in which it finds itself. Essentially these biological parameters are *population structure* and *population size*.

#### VARIATION IN POPULATIONS

Patterns of variation and selection in natural populations have been extensively studied both in nature and in laboratory experiments; and the consequences of natural selection, of genetic drift in small populations, and of their interactions have been worked out, especially by Fisher and by Wright (see reviews by Dobzhansky, 1951, and Stebbins, 1950). Adaptive polymorphisms—genic, chromosomal or balanced—are commonly found in natural populations, as is a high degree of polygenic variation. Much of the variation available for selection is concealed. Controlling factors are mutation rate and selection intensity, inbreeding and the size of the effective population.

Special genetically controlled mechanisms such as dominance, heterosis and canalization have evolved to provide phenotypic stability for the immediate demands of the environment and function also to maintain genetic variability for future evolutionary requirements. In fact the evolution of the genetic code has had to cope with an apparent high rate of intrinsic variation. A single nucleotide substitution in the DNA may not alter the amino acid specification (degeneracy) or, if a different amino acid is inserted in the polypeptide, it will generally be an homologous substitution so that the integrity of the resultant polypeptide is not disturbed.

Genetic variation in a population primarily involves allelic variation at individual loci. It is important to know (*a*) the number of alleles segregating at a locus and (*b*) the proportion of segregating loci. Moreover, we need some indication of what fraction of morphological and physiological variation is genetic in origin.

It is impossible to describe the genotypes of all individuals in a population and the degree to which genotypic differences are manifested phenotypically. However, some progress is being made in understanding the extent of allelic variation in natural populations. Prakash, Lewontin and Hubby (1969) in an extensive analysis of electrophoretic variation in North American populations of *Drosophila pseudoobscura* concluded that on average 42%

of loci were polymorphic and that an individual had 12% of its loci heterozygous. Likewise, H. Harris (1969) finds that for twenty randomly chosen enzymes, for which populations of man have been surveyed for electrophoretic variation, one-third are polymorphic and the mean level of heterozygosity is about 7%.

To what extent allelic variation at this level reflects the relative fitness of contemporary populations is still an open question. Many of the haemoglobin variants found in man (Harris, *loc. cit.*), unlike the classic sickle cell anaemia variant, do not appear to confer a selective disadvantage upon their carriers.

The dependence of heterozygosity and polymorphism upon population size and mutation rate has recently been discussed by Crow (1969). For the sake of simplicity he considers perfectly neutral genes.\* If  $N_e$  is the effective population number and  $\mu$  the mutation rate per locus per generation, then at equilibrium between new mutations and loss of mutants the average heterozygosity  $H$  will be

$$H = \frac{4 N_e \mu}{4 N_e \mu + 1}$$

If  $N_e = 10^4$  and  $\mu = 10^{-4}$ , one would expect 80% of the loci on the average to be heterozygous. At a more conservative assumption of  $\mu = 5 \times 10^{-5}$ , it would require a population of 2,000 to maintain 30% of all loci of an average individual in a heterozygous state.

Polymorphism at the allelic level is measured by the effective number of alleles per locus maintained in the population, essentially by leaving out those with rare representation which contribute little to the population variance. For example, with  $\mu = 10^{-4}$  and  $N_e = 10^4$ , the effective number of alleles is  $(1 - H)^{-1} = 5$ . A large panmictic population will maintain fewer alleles than a number of separate populations of the same total size, "since the different subpopulations will tend to keep different alleles. For example, a population of  $N_e = 10^6$  will maintain about 410 alleles (actual, not effective number) if  $\mu = 10^{-5}$ . If instead there were 1,000 populations of 1,000 individuals each, there would be about 1,300 alleles maintained" (Crow, *loc. cit.*). In other words, in combination, smaller populations tend to maintain a larger number of alleles, though with restricted availability for recombination and co-adaptation. However, if, as is widely accepted, it is not the single allele but the allele in the context of a gene assembly that is the effective adaptive unit, the opportunities for gene flow and co-adaptation may be as relevant as the scale of allelic polymorphism itself.

Recently Ehrlich and Raven (1969), in discussing the relative importance of gene flow and selection in the differentiation of natural populations, assert that gene flow seems to be less important in speciation than has been assumed by pioneers of contemporary evolutionary thought (e.g. Dobzhansky, 1951, p. 164, or Mayr, 1963, p. 21). Ehrlich and Raven present evidence that possibilities of gene flow between natural populations of most species are sharply limited by their isolation; that even species with continuous distribution are not "held together" by gene flow, but on the contrary may exhibit local differentiation; conversely, that some populations separated by virtually insuperable barriers, both in space and in time, are only slightly differentiated from each other. They conclude that "selection itself is both the primary cohesive and disruptive force in evolution: the selective regime determines what influence gene flow has on observed patterns of differentiation".

From this discussion the following conclusions on the *maintenance of variation in natural populations* can be drawn:

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\*Latter (1970) finds that under conditions of centripetal selection the mean level of heterozygosity is not markedly affected.



1. Considerations of variation at the allelic level indicate a minimal population size of the order of thousands rather than hundreds.

2. Although in many species gene flow between populations is normally restricted by distance and breeding behaviour, migration between populations serves as a potential reserve of variation unless precluded altogether by spatial isolation.

3. It follows that a group of populations with potential interpopulation gene flow may have a long-term adaptive advantage over a group of isolated populations even though the latter may maintain a larger number of alleles, and may offer greater scope for fixation of advantageous genes or gene combinations by natural selection and/or genetic drift.

#### CONCLUSIONS: CONSERVATION OF NATURAL COMMUNITIES

1. Wild species can only be preserved *in the context of communities within their natural habitats*. By way of contrast, botanical or zoological gardens provide habitats akin to domestication (cf. p. 162) with the crucial difference that wild plants and animals in captivity are deprived of the range of genetic variation which the breeder provides under domestication. Hence even botanical or zoological gardens with semi-natural conditions cannot provide for more than relatively short-term survival of wild species.

2. In Australia the distribution and abundance of native species are contracting at an increasing rate. *National parks and reserves are "of ever increasing significance in providing sanctuaries for Australia's unique flora and fauna"* (Day, in press). Projecting ourselves a mere century ahead one must assume that reservations will be the only habitats for many or most of the remaining native species.

3. The *size of a reserve* will determine whether all or any of the species it contains are represented at the estimated "minimum viable population" size. Main (1961) and Main and Yadav (in preparation) used the evidence derived from the size, age, topography and flora of offshore islands in Western Australia to ascertain the conditions in which various macropod species were able to survive over extended periods. They concluded that areas of 50,000 acres or over are likely to retain with a minimum of management a representative flora and macropod fauna, *provided the area contains an adequate diversity of soil and topography*. Some species which use rock piles as shelter can persist in small areas, but the smaller the area the more management is required. The minimum viable population appears to lie between 200 and 300 animals, substantially below the population size thought necessary to maintain an adequate level of genetic variation (see p. 165). Clearly the drop-out of individual species, which may endanger the stability of the community as a whole, depends on population size—in the short term in relation to the minimum viable population, in the long term in relation to the population capable of maintaining the minimum level of genetic variation. One may conclude that genetic and evolutionary considerations strongly reinforce the ecological requirement for substantial size.

4. The IBP survey of natural plant communities provides a rational basis for a network of reserves designed to provide for the continuing existence of at least a large proportion of native plants and animals. Many of the communities are included in existing reserves, but few of these are of an adequate size (Australian Academy of Science, 1968). Since their total area is necessarily limited, rationalization of reserves is inevitable if they are to fulfil a long-term function. In a *national plan for long-term conservation* a rational grouping of communities—ideally on the basis of numerical classification—is essential. Commonsense will prevail in ensuring that areas

of specific diversity, such as the upper Richmond and Clarence rivers area with its rich concentration of macropod species (Calaby, 1966) are not overlooked.

5. A national plan for long-term conservation involving large and increasingly scarce habitats of great attractiveness and interest, must face long-term social realities. To exclude or unduly restrict our own species would be as unfeasible and in the long run self-defeating as would be a dense network of roads or heavy grazing by stock. Wise management would provide for *human inclusion rather than exclusion*; indeed, continued existence depends not only on responsibility and insight, but on continuing involvement on the part of the community. Limited economic use is as inevitable, and in the long term advantageous, as is well-designed access for visitors. Nor can an evolutionist be sanguine at the prospect of complete exclusion of immigrant species over long periods—and *our sights should be set for centuries or millennia* rather than decades or generations. Absolute purists think in the short term; the wilderness areas—an admirable concept in itself—are designed for ourselves and our children, but are unlikely to survive for ten thousand years if only because they are not large enough. Nor should the sociological significance of small reserves be underrated. Many may have little to contribute for long-term conservation; but, apart from relieving pressure on larger reserves and giving pleasure and interest to a great many people, the potential educational value of “neighbourhood reserves” is immense. They can contribute materially to the security of major reserves.

#### SPECIES SUCCESSION: EXTINCTION AND EMERGENCE

The decline and ultimate extinction of species as a result of habitat change or restriction is a normal and inevitable event in evolution, and extermination by another species has become common since man's emergence as the predominant species. However, the current rate of species loss has alarmed biologists and saddened nature lovers. Yet we must recognize that the restoration of threatened species to a secure place in natural environments is possible only through restoration and protection of the habitat on the one hand, drastic protection from detrimental agents on the other. How hard it is to secure habitats for threatened plants is well known to conservationists; and the ultimate fate of the polar bear and various species of whales and seals is scarcely in doubt. Rescue for individual threatened species can come from some form of domestication, with the inevitable consequence of selection or genetic drift. The former will occur in true domestication, as for example in the large-scale cultivation of the Californian relic species Monterey pine (*P. radiata*) in Australia and New Zealand; and some day some eucalypt species may have their main distribution in American or African plantations. In small, carefully protected habitat reserves, and even more so in botanical or zoological gardens, populations, of necessity, are small and exposed to the effects of genetic drift. Such rescue operations can scarcely have more than temporary success. Hence preoccupation with the salvage of threatened and vanishing species seems less important than prevention of a similar fate for others, and the creation of conditions for the emergence of new species.

The conditions which are likely to favour the emergence of new species cannot be formulated except in the most general, and obvious, terms. One may assume that habitat and species heterogeneity will be favourable, uniformity unfavourable, the extremes exemplified by tropical rainforest on the one hand, monoculture on the other. It stands to reason that the factors favouring the persistence of existing species are conducive to the emergence of new ones.

## EVOLUTIONARY ETHICS

At long last I shall voice the questions which will have been in your minds throughout this discussion: Why this concern, not only with survival, but with continuing evolution of organisms which are of no earthly use to ourselves? Is this not contrary to the evolutionary trend which has established man in control of all—or most—other biota, whose continued existence therefore is subject to the interest of the dominant species? Here are my personal answers:

1. Evolution is not something remote in time and infinitely slow in progress. It is a continuing process and, as Barber (1949) has pointed out, can be very rapid in action. It is always with us.

2. Man's control over heredity and environment is increasingly taking the place of natural selection. Domesticated plants and animals have altogether lost the capacity for existence—let alone continuing evolution—without human assistance; and environments have been so widely and drastically modified that large numbers of wild species have been exterminated through loss of habitats. Of the 119 marsupial species of Australia, Calaby (1963) listed five as extinct and 34 as endangered. As Frith (1969) reported in the last Macleay Memorial Lecture, the rich mammalian fauna in the Riverina, Sir William's home territory, had been recorded, but never properly surveyed and classified; it has now almost entirely disappeared with the exception of red and grey kangaroos. According to J. H. Willis, quoted by Turner (1966), 12 endemic plant species in Victoria are extinct, 36 nearly so, and 201 are restricted to a few colonies or individual specimens. Species, and genera, have always disappeared in the course of evolution; but the current rate of destruction combined with the alienation of living space for potential replacements, is indubitably without parallel in the history of evolution. If this trend continues for another century, *few species will remain which are not either of actual or potential use to man, or which for the time being he is unable to subdue or exterminate.*

3. The question is: do we wish to create a way of life in which all—or nearly all—living beings serve our purposes, all variation is at our command, evolution of all life is at the will of man? Clearly this is the point of decision: over large parts of the earth, including Australia with its vulnerable environment, it is not as yet too late, but it soon will be. *The decision cannot be long delayed.*

4. No longer can we claim evolutionary innocence. We are still subject to evolutionary processes (though we may gain a measure of control before long), but we are also major operators. We are *not* the equivalent of an ice age or a rise in the sea level: we are capable of prediction and of control. *We have acquired evolutionary responsibility.*

5. The present situation is unprecedented in history, and of unparalleled gravity. Never before have a mere one or two generations faced such responsibility. For let us understand this clearly—Nigel Calder's utopia of a wilderness recovery is a fantasy, at least for Australia: most of the changes which are taking place are irreversible. They are there for all time. *Our decision involves the distant future.*

6. The fate of all forms of life, of wild and domesticated plants and animals and doubtless of our own species—and of the environments in which they exist—depends on the *continuity of variation*. At the entrance to CERES, the Controlled Environment Research Laboratory in Canberra, there is the following inscription: "Cherish the earth, for man will live by it forever." We might have said with equal justification: "Cherish variation for without it life will perish."

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